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AUSTRALIAN CARABID BEETLES X. *BEMBIDION*

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This is the tenth in a series of papers on Australian Carabidae. Some earlier parts, including a list of localities at which I collected in 1956-1958 and a discussion of transition of wet forest carabid faunas from New Guinea to Tasmania, are given under References.

The present paper deals with the Australian species of *Bembidion* (*sensu lato*). This is a zoogeographically important genus, which tends to be bi-zonal in distribution, occurring mainly in the north and south temperate zones of the world (Darlington 1959, pp. 332-333). The distribution, ecology, relationships, and possible history of the Australian forms are therefore noteworthy and will be summarized after discussion of the separate species.

I am indebted to Prof. Carl H. Lindroth for dissecting males of all the Australian species and telling me how he thinks they are related to European and North American forms. I could have made the dissections myself, but I am not familiar with the genitalic characters of northern *Bembidion* and could not have interpreted the characters of the Australian species. However, neither Prof. Lindroth nor I have investigated most of the Asiatic species or those of New Zealand or southern South America. This paper is therefore only a limited contribution to the zoogeography of *Bembidion*.

At the time of Sloane's last study of Australian Bembidiini (1921), he knew five Australian species of *Bembidion* and two of *Cillenus*. Two supposed "*Bembidion*" of Blackburn's that Sloane did not know (*hobarti* and *wattsense*) are in fact not *Bembidion* but *Tachys*. I plan to treat them in my next paper. I have series of all five real *Bembidion* known to Sloane and

have seen no other native species, and it may be that these five species of the genus (excluding *Cillenus*) are all that are native in Australia, although it is too soon to be sure about this. References and synonymy of the species are given by Sloane (*op. cit.*) and will usually not be repeated here. The species should be identifiable by the following key, which is based partly on Sloane's key (1921, p. 193). All the species are winged and presumably able to fly, except that the wings are dimorphic in *proprium* (*q.v.*).

Key to Australian Species of Bembidion

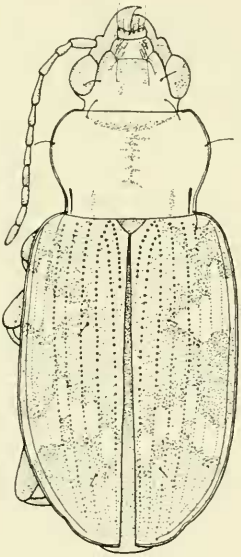
1. Large (*c.* 5.2-6.5 mm.); dull bronze, elytra with 2 incomplete transverse pale fasciae; clypeus with several fine converging grooves on each side (introduced from South America) . . . . . *brullei*
— Smaller; not marked as above; (native) 2
2. Frontal sulci long, impressed and converging on clypeus; upper surface of insect dull or shining; elytron with 6 or 7 dorsal striae 3
— Frontal sulci shallow and rather short, not crossing clypeus; upper surface dull; elytron with 7 dorsal striae 5
3. Dull brown with vague paler elytral markings; whole upper surface microreticulate; elytron with 6 dorsal striae (stria 7 absent or faint); length *c.* 4.2-4.8 mm. . . . . *errans*
— Shining, upper surface not microreticulate; elytron 7-striate; size smaller 4
4. Elytron with 2 seta-bearing punctures on 3rd interval, none on 5th; color black, elytral apices and sometimes lateral subapical spots slightly paler; length *c.* 3.3-3.9 mm. . . . . *blackburni*
— Elytral intervals 3 and 5 each with several inconspicuous seta-bearing punctures; color irregular dark brown; length *c.* 2.9-3.4 mm. *proprium*
5. Prothorax transverse, sides not sinuate posteriorly; color much like following species except apical testaceous area of each elytron broken into subapical and apical marks which are often narrowly connected along outer elytral margin and sometimes connected near suture too; length *c.* 3.0-4.0 mm. . . . . *jacksoniense*
— Prothorax cordate, sides sinuate posteriorly; color greenish or bronzed with elytral apices conspicuously testaceous, the testaceous areas broadly lunate; length *c.* 4.0-4.7 mm. . . . . *opulentum*

Bembidion (Notaphus) brullei (Gemminger and Harold)

variegatum Brullé 1843, p. 44 (not Say).
Bembicidium brullei Gemminger and Harold 1868, p. 409.

Form as figured, broader and less convex than usual in Australian species of genus; bronze, appendages irregularly testaceous and fuscous, elytra with complex but variable pale

marks which usually involve epipleuri, parts of elytral bases inside humeri, marginal channels, apices (rather vaguely), an irregular interrupted fascia before middle often including very elongate pale areas on intervals 7 and 8 and isolated spots on 3rd intervals, and an irregular incomplete post-median fascia; sides of abdomen also pale; upper surface dull, with close reticulate microsculpture, isodiametric on head and pronotum, vaguely



Bembidion brullei (Gemminger and Harold), from between Murray Bridge and Meningie, South Australia.

transverse (but nearly isodiametric) on elytra. *Head* .76 and .76 width prothorax (in ♂ ♀ measured); eyes large and prominent; antennae of moderate length, middle segments *c.* 2½X long as wide; front slightly convex; frontal grooves subparallel (slightly curved) and poorly defined on disc, converging and more sharply impressed across clypeus, and latter with additional fine longitudinal (converging) grooves or wrinkles; mentum with entire tooth. *Prothorax* transversely subcordate with rather broad base; width/length 1.45 and 1.44 (in measured ♂ ♀); base/apex 1.19 and 1.17; base/head 1.07 and 1.06; sides broadly arcuate for much of length, moderately sinuate before basal angles; latter well defined and nearly right or slightly

obtuse; lateral margins moderate, each with usual 2 setae; disc convex, with anterior transverse impression poorly defined, middle line distinct but slightly abbreviated at both ends, basal transverse impression poorly defined; baso-lateral impressions deepest inwardly, bottoms irregular or slightly convex, slightly wrinkled but not much punctate, limited externally by longitudinal carinae distinct from prothoracic margins. *Elytra c.* ⅓ wider than prothorax (E/P 1.36 and 1.35); humeri prominent but rounded; sides subparallel for much of length; margins moderate (wider than in *opulentum*), ending anteriorly opposite ends 6th striae (opposite 5th in *opulentum*), forming translucent shelves before subapical sinuations; striation entire, striae slightly impressed and rather strongly punctate especially on disc; intervals slightly convex, 3rd with 2 seta-bearing punctures about ⅓ from base and less than ⅓ from apex. *Inner wings* fully developed. *Lower surface* microreticulate but mostly not distinctly punctate; anterior process of metasternum strongly margined between middle coxae, the margin strongly rounded-angulate at middle. *Legs* without obvious distinctive characters. *Secondary sexual characters:* ♂ with 2 segments each front tarsus moderately dilated and squamulose below; ♂ with 1, ♀ 2 setae each side last ventral segment. Length *c.* 5.2-6.5; width *c.* 2.0-2.6 mm.

Known in Australia only from six specimens taken by myself beside the road between Murray Bridge and Meningie, South Australia, September 1957, probably beside one of the series of more or less saline lakes near the mouth of the Murray River. However, my collecting there was done under difficulty, in the face of light rain driven by strong wind, and I did not distinguish the species in the field. Specimens of *Bembidion errans* and *proprium* were taken on the same occasion.

Superficially, this species looks rather like *Bembidion* (*Notaphus*) *dentellum* Thunberg and related species of the Northern Hemisphere, and Prof. Lindroth says its genitalic characters are those of a true *Notaphus:* "The armature of the internal sac, even in details, comes very close to that of *approximatum* Lec. and *coloradense* Hayw." of North America. The sculpture of the clypeus of *brullei* is distinctive but, I think, not of subgeneric value.

I was on the point of describing this as a new Australian species when I discovered specimens of it in the Museum of

Comparative Zoology from South America, from several localities in northern Argentina. It was described more than a hundred years ago from specimens taken on the seashore at Montevideo, and it is apparently common in the La Plata region and at Córdoba, Argentina. It has presumably been introduced into southern Australia by shipping.

Bembidion (Ananotaphus) errans Blackburn

Netolitzky (1931b, pp. 181-182) made this the type of subgenus *Ananotaphus,* which may be considered to include also the two following species: *proprium* Blackburn and *blackburni* Csiki. The three species in question are somewhat alike in form and agree in having deep frontal sulci, and the male genitalia "show a certain, though not very evident, agreement in the internal sac" (Lindroth). However, the three species differ considerably among themselves, and their relationship to other subgenera is doubtful, so far as the genitalic characters are concerned.

Blackburn and also Sloane (1921) thought that *errans* occurred only near the coast, and I agree, although it is not confined to obviously saline habitats. It has been previously recorded from southern Western Australia, South Australia, and Victoria. I have a series from southern Western Australia, from several localities including the vicinity of Perth and Pemberton, collected by H. Demarz, and I took two specimens between Murray Bridge and Meningie, South Australia, and four near Hobart, Tasmania. In Western Australia Sloane found it "on the muddy margin of the Vasse River within the tidal influence," and some of Demarz's specimens were taken at Mandura salt lake. My South Australian specimens were probably taken by slightly saline ponds near (east of) the mouth of the Murray River (see under preceding species). My Tasmanian specimens were on the grassy-muddy bank of a small pond in flat, lowland country north of Hobart. This was essentially a fresh-water habitat, but it was only a few miles from the coast and there may have been a trace of salt there. A series of *B. proprium* and one specimen of *blackburni* were taken at the same place.

Bembidion (Ananotaphus) proprium Blackburn

Sloane (1921) knew this species too only from localities on or near the coast of southern Australia, including South

Australia, Victoria, and southern New South Wales (Wollongong). One of his specimens was "beside a little rivulet near where it entered the sea" (presumably at Wollongong). My mainland specimens too are from coastal localities, from between Murray Bridge and Meningie (see under *B. brullei*) and between Meningie and Kingston, South Australia (taken by myself), and from Seaford, Victoria (taken "under beach drift" by W. L. Brown). However, I took a series in Tasmania, north of Hobart, beside fresh water, though still near the coast (see under *errans*). The species thus seems to have about the same ecological distribution as *errans*.

My seven mainland specimens are all fully winged. Most of the sixteen from Tasmania have the inner wings somewhat reduced, about as long as the elytra, slightly folded or crumpled at apex, and evidently unfit for flight, but one of the Tasmanian specimens is fully winged or nearly so.

Bembidion (Ananotaphus) blackburni Csiki

Csiki 1928, p. 159.
dubium Blackburn 1888 (not Heer, not Wollaston).

Sloane (1921) records this species from South Australia, Victoria, and southern New South Wales, and notes that it occurs beside fresh water, in some cases much farther from the coast than the preceding species. I took it at Winchelsea, Victoria, and found it common in Tasmania. It occurred in wet places at low altitudes near Hobart (see under *errans*) and near Ellendale, but it was commoner on the mountains, near Lake St. Clair (over 2400 ft. altitude) and Great Lake (*c.* 3400 ft.), for example. On the mountains in Tasmania *blackburni* occurs not only beside standing water and in other wet places but sometimes also on wet, open heaths near and above tree line. Here it runs in sunlight in and on the dense mats of moss and other vegetation that cover much of the ground in open places. This is a true subantarctic habitat. *Bembidion blackburni* is the only Australian species of the genus that reaches a subantarctic habitat.

On the wet mountain heaths, *B. blackburni* is a member of a small association of superficially similar species of small black Carabidae including *Cyphotrechodes gibbipennis* (Blackburn), *Amblystomus nigrinus* Csiki (*niger* Blackburn), and *Euthenarus nigellus* Sloane. These species look so much alike, superficially, that it is not easy to distinguish them in the field with the naked

eye. They occur together on warm days on wet moss pads, etc., on the mountain heaths as well as in other wet places. This is a striking example of convergence of species of unrelated carabid genera. I do not know its ecological significance. I should add that, although these species occur together under some circumstances, they do not have identical ecological limits elsewhere.

Bembidion (Philochthus) jacksoniense Guérin

[Subgenus *Sloanephila* Netolitzky is here declared a synonym of *Philochthus*, for reasons given below (new synonymy).]

See Sloane (1921, p. 193) for synonyms and references, and see Netolitzky (1931b, p. 182) for subgenus *Sloanephila*, based on this species. However, Netolitzky himself notes the great similarity in most characters of *jacksoniense* and species of the northern (Europe, western Asia, North Africa, etc.) subgenus *Philochthus*, and Prof. Lindroth finds "general agreement in the arrangement of the internal sac of the male genitalia in *jacksoniense* and subg. *Philochthus* . . . ," and it seems to me there is more to gain by recognizing the relationship and putting *jacksoniense* in *Philochthus* than by stressing the differences. Netolitzky says the principal difference is that the metasternal process between the middle coxae is margined in the northern *Philochthus*, not in *jacksoniense*. Netolitzky adds that in this character and in frontal sculpture *jacksoniense* closely resembles *B. "Notaphomimus"* (=*Notaphocampa*) *opulentum* (below). I think these facts may indicate (1) a close relationship between *jacksoniense* and the northern *Philochthus* and (2) a less close one between *Philochthus* and *Notaphocampa*, with *opulentum* perhaps in some ways a connecting link.

Sloane says *jacksoniense* is found over the whole continent of Australia, beside fresh water, and this is probably essentially true. However, it may be absent in small areas in the east and perhaps in larger ones in the north (I am not sure about this) and it has not yet been found in Tasmania, and it certainly occurs in brackish and perhaps alkaline habitats (inland) as well as by strictly fresh water. It is very common in Western Australia but less so in the east, although I have specimens from several eastern localities ranging from Townsville in tropical Queensland south to the Blue Mountains of New South Wales and Mt. Kosciusko. In some localities it occurs with the following species, *opulentum*. In light-trap material from Cooper Crossing, Lake Eyre, it is represented by a few specimens among many *opulentum*.

Bembidion (Notaphocampa) opulentum Nietner

[Subgenus *Notaphomimus* Netolitzky is here declared a synonym of *Notaphocampa*, for reasons given below (new synonymy).]

sobrinum auct. (not Boheman).

Sloane (1921, p. 193) gives Australian synonyms and earlier references to this species. Netolitzky (1931b, pp. 175-178) makes an (I think) unnecessary special subgenus, *Notaphomimus,* for it. Except for the difference in frontal sculpture, which I think is over-stressed by Netolitzky, *opulentum* seems very close to *Bembidion* (*Notaphocampa*) *niloticum* Dejean, and the two species are closely allied in genitalic characters (Lindroth).

I have discussed the distribution of *opulentum* (*"sobrinum"*) recently (1959, p. 339), but my statement that the species ranges from Africa through tropical Asia, etc., was apparently wrong, although made on good authority (Netolitzky, Andrewes). There seem to be two slightly different species: *foveolatum* Dejean (*sobrinum* Boheman) of Africa, Madagascar, etc., and *opulentum* Nietner of the Oriental-Australian region (see Jeannel 1946, pp. 370-371, and Basilewsky 1952, p. 177). *B. opulentum* occurs through tropical Asia, part (but not all) of the Malay Archipelago, part of tropical and south temporate eastern Australia, and apparently also in New Caledonia. It exhibits some geographical variation (Netolitzky, *loc. cit.*): the Australian form can be called subspecies *riverinae* Sloane. In Australia it is widely distributed in the eastern part of the continent at least from the latitude of Townsville south to Tasmania and west to South Australia, but I do not think it has yet been found in Western Australia. (Sloane knew it only from Queensland, New South Wales, and Victoria.) It usually occurs near the margins of standing or slowly moving fresh water. Six specimens that I took behind the bank of the Burdekin River near Charters Towers, Queensland, in March 1958, were running on wet mud and beside a stagnant pool of flood water. A specimen from near Waratah, Tasmania, was taken on a log floating in water at the side of a small pond. And three from west of Renmark, South Australia, September 1957 were, I think, taken on mud behind the bank of the Murray River. However, the species apparently occurs also in inland saline areas, for I have a long series taken at light at Cooper Crossing, Lake Eyre, South Australia, in February 1956 (collected by Dr. G. F. Gross). That this species is so widely distributed in Asia but has not yet spread through the whole of Australia suggests that it has reached Australia

comparatively recently, possibly by way of the Lesser Sunda Islands and Timor, for it does not seem to occur in New Guinea or Cape York.

Bembidion, subgenus Cillenus

Cillenus is commonly considered a subgenus of *Bembidion*. Its gross range is from Europe and China to Australia, Tasmania, and New Zealand, but it is strictly coastal. Different species of it occur by running water near the coast, or on ocean beaches, or actually between the tide lines. I have discussed its distribution and possible history elsewhere (1953; 1959, pp. 333-334).

Two species of *Cillenus* are known from (eastern) Australia: a larger, duller one (*albovirens* Sloane) from tropical Queensland (from Townsville, *not* Cairns as incorrectly stated by Sloane in 1921), and a smaller, more slender, more shining one (*mastersi* Sloane) from Sydney and the north coast of Tasmania. Both species probably live on the ocean beach. Both are (irregularly) testaceous, as beach-living Carabidae often are. Both Australian species are fully winged and one or both probably fly. My single specimen of *albovirens* probably flew to light at Townsville, although I did not actually see it do so. Some other *Cillenus* in other regions including New Zealand are flightless.

SUMMARY AND DISCUSSION

The five native Australian species of *Bembidion* (excluding *Cillenus,* which has evidently had an independent history) are distributed as follows. The three species of subgenus *Ananotaphus* occur in the southern part of Australia, and all of them extend to Tasmania too. Of these three, *errans* and *proprium* apparently occur only at low altitudes near the coast, sometimes in saline but also sometimes in fresh or nearly fresh habitats beside water, while *blackburni* is more widely distributed. It sometimes occurs at low altitudes with the two other species, but it has also entered the subantarctic zone on Tasmanian mountains. *B.* (*Philochthus*) *jacksoniense* occurs almost throughout Australia (but not Tasmania) in both fresh and saline (interior) habitats, usually beside standing or slowly moving water. And *B.* (*Notaphocampa*) *opulentum* is widely distributed in the Orient and in tropical and south temperate eastern Australia. It reaches Tasmania but apparently not Western Australia. It occurs in about the same variety of habitats as *jacksoniense*.

These five native Australian species of *Bembidion* are apparently descended from three successive invaders. The first was the ancestor of the endemic subgenus *Ananotaphus*, which has differentiated in Australia and formed three very distinct species. All three are now confined to the southern edge of Australia plus Tasmania; one of the three (*blackburni*) extends into subantarctic habitats on mountains in Tasmania; and one (*proprium*) is undergoing wing atrophy. This looks like an early stage in penetration of the southern cold temperate zone by an originally tropical or northern winged group of Carabidae, and evolution of a derivative flightless stock adapted to southern cold temperate habitats. The ancestor(s) of the Australian and Tasmanian "*Trechus*" may have gone through a stage like this.

The second invader was the ancestor of *Bembidion* (*Philochthus*) *jacksoniense*. The latter has spread throughout Australia (but not Tasmania) and is now a thoroughly distinct species, although its relationship to the northern species of the subgenus is still clear. In southern Australia it overlaps the edge of the range of the species of *Ananotaphus* but (in my experience) it does not often actually occur with them and perhaps does not compete with them very much now, although it may limit their distribution northward.

The third invader is *Bembidion* (*Notaphocampa*) *opulentum*. The fact that this species is now widely distributed in southern Asia (with a very close relative in Africa) but has apparently not yet spread through the whole of Australia, and the fact that the Australian population is only subspecifically differentiated, suggest that the species has reached Australia rather recently. In eastern Australia it occurs with *jacksoniense*, in the same habitats. The two species may compete, and *opulentum* may be replacing *jacksoniense*, which seems to be much less common in eastern Australia, where *opulentum* occurs, than in the west, where *opulentum* does not occur.

This history of three successive invasions, the later invaders perhaps competing with and modifying the distributions of earlier ones, accounts very well for the present distribution of *Bembidion* in Australia. The question then is, what has been the history of the ancestral forms outside Australia?

Bembidion is now dominant in the north temperate zone but is very poorly represented in the tropics, where the genus is replaced by swarms of *Tachys*. The obvious, but not necessarily the correct, guess, therefore, is that the three *Bembidion* that have invaded Australia have somehow crossed the tropics from

the north temperate zone. This would be consistent with the distribution of *Philochthus,* which is now wholly north temperate except for *jacksoniense* isolated in Australia.

However, another, perhaps more probable history can be suggested. The endemic Australian subgenus *Ananotaphus* vaguely resembles *Notaphocampa* in form. *Ananotaphus* has deep frontal sulci and *Notaphocampa opulentum* has shallow ones, but *opulentum* is very close to *Notaphocampa niloticum* Dejean in most characters including male genitalia (Lindroth), and *niloticum* has deep frontal sulci. *Ananotaphus* and *Notaphocampa* are in this way linked by *niloticum,* which, incidentally, ranges from North Africa across tropical Asia north to temperate Japan. Similarities between *Notaphocampa opulentum* and *Philochthus jacksoniense* are noted under the latter in the preceding pages, and *jacksoniense* is clearly related to northern species of *Philochthus.* These are hints that *Ananotaphus, Notaphocampa,* and *Philochthus,* which include all the *Bembidion* (except *Cillenus*) native in Australia, *may* belong to one group which has had a rather complex evolutionary and geographical history, and the group may have been primarily tropical. *B. opulentum* and *niloticum* are widespread in the tropics now; all the Australian *Bembidion* are salt-tolerant, which is characteristic of tropical *Bembidion* (Darlington 1953, p. 14), and at least one European *Philochthus* (*aeneum* Germar) is salt-tolerant too (Lindroth); and evolution in the tropics would facilitate the successive invasions of Australia that have occurred.

I suggest, then, that subgenera *Ananotaphus, Philochthus,* and *Notaphocampa may* all be derived from one salt-tolerant group of *Bembidion* that has evolved primarily in the Old World tropics, has invaded Australia three times, and has invaded the north temperate zone at least twice, once as *Philochthus* in Europe, etc., and once as *Notaphocampa niloticum* in Japan. This hypothetical history cannot be critically tested until the phylogeny of the whole genus *Bembidion* is better understood. Genitalic characters do *not* clearly confirm it. If the forms in question have evolved as suggested, their history has probably been complex and may have involved additional groups of *Bembidion* that have not reached Australia.

Cillenus is another, independent subgenus of *Bembidion* (perhaps it should be considered a related genus) that has crossed or evolved in the tropics, in saline habitats, and reached Australia (Darlington 1953: 1959, p. 333).

It is noteworthy that, although several stocks of *Bembidion* have reached the western part of the Malay Archipelago from Asia apparently by "mountain hopping," by somehow dispersing from mountain to mountain and from island to island at considerable altitudes (Darlington 1959), none has reached Australia or New Guinea in this way. No *Bembidion* has been found on mountains in New Guinea, and the Australian species are primarily lowland forms and seem to be descended from salt-tolerant ancestors that crossed or evolved in the tropics at low altitudes.

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